

The Evolution and Social Significance of the Ant Proventriculus

By T. EISNER AND W. L. BROWN, JR.¹

Harvard University
Cambridge, Mass.

ABSTRACT

The evolution of the ant proventriculus as a valve-dam guarding the posterior outlet of the crop is correlated with the development of the crop as a social storage organ. The primitive ant proventriculus (subfamilies Myrmecinae, Pseudomyrmecinae, Aneuretinae, Ponerinae, and Cerapachyinae) is thin-walled and flaccid, and therefore ill-adapted to dam the crop without enforcement from sphincter muscles. Ants having such proventriculi have failed to develop "replete" castes. In the specialized Formicinae and Dolichoderinae, proventricular damming no longer depends on sustained sphincter contraction; the proventricular framework is rigid and sclerotized, and constructed in such a way as to be virtually impervious to leakage. The true known "replete" castes are all found in one or the other of these two subfamilies.

In the subfamilies Dorylinae and Myrmicinae, many genera show reduction of proventricular components to the point where the proventriculus is little more than a posterior constriction of the crop. The functional significance of this degeneration remains speculative at present.

A dendrogram is presented, outlining presumed formicid phylogenetic relationships, as based largely on the proventriculus.

The Hymenoptera, like many other insects, have two central chambers in the digestive tract—the crop, followed by the midgut (Fig. 1). The midgut is the true digestive and absorptive organ. In order to operate efficiently, the midgut requires a relatively constant flow of nutrient material. But in the Hymenoptera, the adult is normally an active stage with necessarily discontinuous feeding habits. The opposing requirements of adult activity and midgut operation are met by the interposition of a sac-like antechamber to the midgut—the crop.

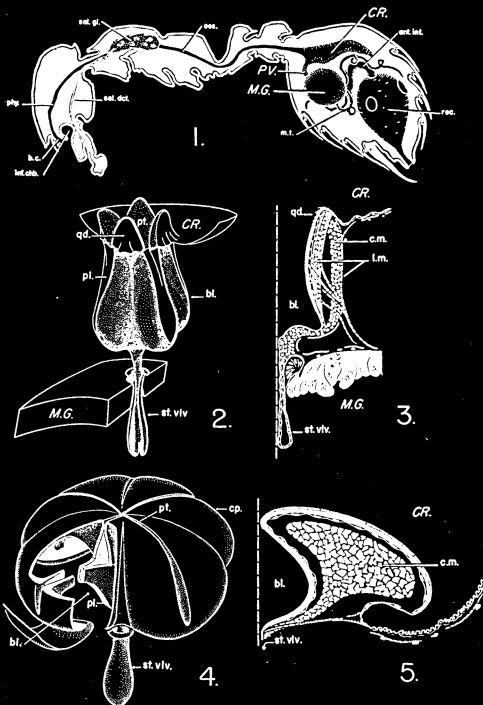
At feeding, the crop becomes gorged with fluid nutrient, and this fluid is then passed slowly, in controlled amounts, to the midgut, via the narrowed valvular connection called the proventriculus (Fig. 1). As usually developed, the proventriculus of adult Hymenoptera is no mere strait between crop and midgut; rather it is provided with both dam-effecting sphincter muscles, acting to stem the pressure exerted by the fluid crop contents and with a muscular pump-like bulb, which is brought into action whenever fluid is to be passed to the midgut.

In the social Hymenoptera, continued evolution has placed a premium on the storage of nutrients for the benefit of the society as a whole. In the social bees, storage is accomplished by deposit of nutrients in receptacles constructed within the hive. In the higher ants the storage problem has been solved primarily by structural improvement of the storage capabilities of the individual worker crop, which increasingly moves into the role of a "social stomach". The enhanced storage ability of the crop is clearly significant as a basis for the development of complex patterns of oral food exchange between the foraging and non-foraging nestmates. This exchange is one of the most fundamental bonds in the social organization of ants (Wheeler 1923; Le Masne 1953; Eisner and Wilson 1958; Wilson and Eisner 1957).

Improvement of the crop involves, in some cases, an increase in volume capacity. But probably more important have been structural modifications of the proventriculus that allow the crop to remain full for longer periods of time. In brief, these modifications have all been in the direction of replacement of the fatigue-prone muscular valve closure by a system in which the dam is effected passively by the structure itself. Since the passive dam also blocks the ant's supply of nutrient to its own midgut, elaborate refinements of the pumping mechanism were evolved to pass nutrients through the dam when necessary to the requirements of the individual.

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The passive-dam proventriculus has reached its highest development in the Dolichoderinae and in the Formicinae, and it is in these subfamilies that the special *replete* caste—workers with crops and gasters capable of great and prolonged distention—has been perfected. Such repletes are a functional analogue of the bees' honeycomb, and are undoubtedly a factor helping the colony to pass unfavorable seasons.



These are some of the conclusions reached after a detailed comparative study by one of us (Eisner 1957), involving an analysis of structure, explanation of function, and evaluation of phyletic relationships for each of the principal kinds of proventriculus known among the ants. About 50 genera were investigated, representing 8 of the 9 subfamilies. The aim of the present paper is to exemplify these studies through the brief consideration of the most strategic evolutionary types of ant proventriculi.

Every proventriculus consists essentially of a central cuticular framework, and an outer envelope of muscles. The relationships of these two components were determined from serial sections. Additional preparations were made, consisting of whole mounts of the isolated cuticular framework, divested of all attached muscles by treatment with hot 10% KOH. The illustrations are of two types. One type depicts the isolated framework, sometimes in exploded view, or with some sections cut away, so as to clarify structural intricacies. The other type shows the intact proventriculus, with all attached muscles, as it appears in longitudinal section.

THE GENERALIZED FORMICID PROVENTRICULUS: MYRMECIA

The Australian genus *Myrmecia* shows many of the features of morphology and behavior expected of a generalized ant. Regurgitative feeding is poorly developed, and the workers act more as individuals than do the workers of the higher ants. The proventriculus is a simple structure. The cuticular framework (Fig. 2) consists of a relatively thin-walled, flask-shaped bulb (bl.), with a wide anterior inlet orifice, or portal (pt.), and a slender, flexible outlet tube, the stomodæal valve (st. viv.). The walls of the bulb are four broad, sclerotized plates, joined by narrow longitudinal strips of thin flexible cuticle, the plicæ (pl.). Anteriorly the bulbar plates project into the lumen of the crop as four apically rounded lobes, or quadrants (qd.), that frame the portal orifice. The bulb is surrounded by a powerful set of circular muscles, and several groups of longitudinal muscles (Fig. 3, c.m., l.m.).

This type of proventriculus is identical in all major respects to that of aculeate Hymenoptera other than ants. Among the ants it is found not only in the Myrmecinae, but is preserved in essentially unmodified form in the Ponerinae, Cerapachyinae, Pseudomyrmecinae and Aneuretinae studied by us.

Our interpretation of the pumping cycle of this type of proventriculus is as follows. The intake phase is initiated by the longitudinal muscles; the plates of the bulb are pulled apart causing the plicæ to unfold, and crop fluid is sucked through the widened portal into the expanded bulb. The longitudinal muscles then relax in favor of the antagonistic circular muscle complement, which contracts in its turn; the bulb is squeezed and its contents are forced back through the stomodæal valve into the midgut. A significant return flow into the crop is hindered by the tight closure of the portal through approximation of the quadrants.

This type of organ is adapted to serve short-term crop-damming needs, but is inadequate for prolonged damming. Neither the portal nor the stomodæal valve seem capable of a sufficiently tight closure to stem crop fluid pressure without enforcement from the circular muscles. The length of time over which the crop can be maintained full of fluid is therefore dependent on the endurance of the muscles that maintain the dam. That prolonged crop storage actually never occurs in ants having this type of proventriculus is strongly suggested by the fact that none of them, as far as is known, have evolved true "replete" castes.

Fig. 1. Digestive tract of the ant *Myrmica rubra* (simplified, with some cephalic structures omitted, after Janet); ant. int., anterior intestine; b. c. buccal cavity; CR., crop; inf. chb., infrabuccal chamber; M. G., midgut; m. t., malpighian tubule, oes.; oesophagus; ph., pharynx; PV., proventriculus; rec. rectum; sal. d., salivary duct; sal. gl., salivary gland.

Fig. 2. Cuticular framework of the proventriculus of *Myrmecia regularis* Crawley; bl., bulb; CR., crop; M. G., midgut; pl., plicæ; pt., portal; qd., quadrant; st. viv., stomodæal valve.

Fig. 3. Longitudinal section through the proventriculus of *Myrmecia vindex* F. Smith; c. m., circular muscles; l. m., longitudinal muscles; other lettering as in Fig. 2.

Fig. 4. Cuticular framework of the proventriculus of *Iridomyrmex detectus* (F. Smith). Lettering as in Fig. 2.

Fig. 5. Longitudinal section through the proventriculus of *Iridomyrmex detectus* (F. Smith); Stomodæal valve omitted. Lettering as in Figs. 2 and 3.

THE ADVANCED DOLICHODERINE PROVENTRICULUS: *IRIDOMYRMEX*

Passing over a number of lower dolichoderines with intermediate proventricular plan (Fig. 9), we come to *Iridomyrmex*, which has the most highly evolved proventriculus known among the dolichoderines.

In *Iridomyrmex*, the proventricular framework (Fig. 4) is strong and rigid enough to preclude all but the most narrowly restricted movement of its parts. The quadrants are stiffened and fused together, leaving only a narrow pile-line cruciform slit to represent the gaping portal of *Myrmecia*. Collectively, the quadrants form a dome, or cupola (cp.), extended to cover and completely receive the chamber of the bulb and its surrounding muscles. The bulb itself is fully sclerotized throughout; there are no longer present the flexible plicae found in *Myrmecia*. The muscles are interesting, for while they are very powerful, they now consist only of circular elements (Fig. 5). The longitudinal muscles have become useless, and are lost, since the portal is immovable, and the necessary antagonism to the circular muscles now resides in the intrinsic "spring" of the cuticular framework.

In spite of the radical structural innovations of the *Iridomyrmex* proventriculus, bulbar operation remains quite similar to what it is in *Myrmecia*. One difference is that in *Iridomyrmex* bulbar expansion occurs passively, by elasticity, rather than under tension from longitudinal muscles. A second difference is that during bulbar intake it is no longer possible to widen the portal. The negative pressure exerted by the expanding bulb provides all the suction necessary to draw fluid through the portal slits into the bulb.

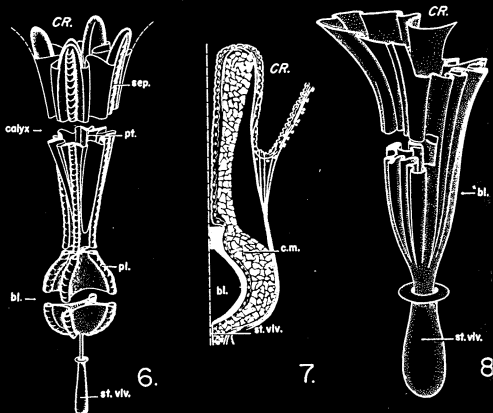


Fig. 6. Exploded diagram of the sepalous formicine proventriculus (based on *Camponotus*; may be taken also to approximate *Formica*); sep., sepal; other lettering as in Fig. 2.

Fig. 7. Longitudinal section through the proventriculus of *Formica* (*fusca* group); stomodaeal valve omitted; lettering as in Figs. 2 and 3.

Fig. 8. Cuticular framework of the proventriculus of *Eciton hamatum* (Fabricius); lettering as in Fig. 2.

But as regards the ability to dam the crop, *Iridomyrmex* shows great improvement over *Myrmecia*. In *Iridomyrmex* the resting proventriculus can effectively restrain the crop pressure without any sphincter enforcement whatsoever. The rigid, densely pilose, and exceedingly narrow portal cleft is in itself capable of stemming crop pressure and preventing leakage to the midgut. In fact, fluid can probably be passed through the portal slits only under suction from the bulb when the active proventriculus prevails in its function as a pump.

THE ADVANCED FORMICINE PROVENTRICULUS: *FORMICA*

The formicine proventriculus has evolved independently from that of the dolichoderines (Fig. 9). Again we omit a series of intermediate stages, to pass on directly to a representative of the most advanced type within the lineage.

In the proventriculus of *Formica* (Fig. 6), the four corners of the bulb have been drawn out forward, away from the bulb, as long arms, or sepals (sep.), collectively constituting the calyx. Each sepal carries along its inner face the corresponding extension of the cruciform portal slit. Down the inside of each sepal runs a long canal to which the pile-guarded slit communicates, and which opens posteriorly into the bulb lumen. This proventriculus, like that of *Iridomyrmex*, is rigidly sclerotized throughout. The plicae of the bulb are sclerotized and act as spring-antagonists to the circular muscles during bulb expansion; as in *Iridomyrmex*, there are retained no longitudinal muscles for bulb expansion (Fig. 7).

In bulbar operation, *Formica* is quite similar to *Iridomyrmex*, except that the sepals, with their slits and canals, provide a new route for bulbar intake. As regards damming ability, *Formica* has evolved the same narrow, rigid, slit-like portal as *Iridomyrmex*, and is therefore equally well adapted to serve as a passive dam.

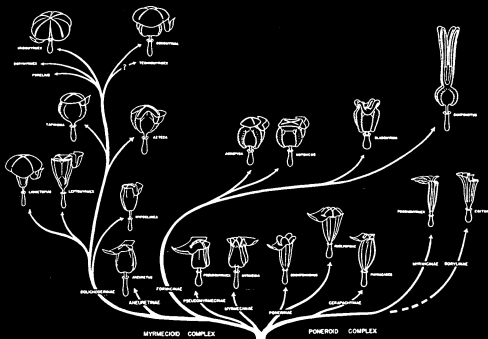


Fig. 9. Dendrogram showing evolution of the formicid proventriculus.

If we compare *Iridomyrmex* and *Formica*, it becomes apparent that in spite of their obvious structural dissimilarity, they are actually remarkably similar as regards their functional attainments. Both have met the need for passive damming by reducing the portal to a narrow, permanently immobile slit. In so doing, both were faced with the diffi-

culty of providing adequate portal area for bulbar intake. This difficulty was solved by increasing the portal slits in length, and not in width. Width increase would have conflicted with the damming requirements. In *Formica* the portal slits are lengthened by extending them forward over the sepals. In *Iridomyrmex* they are lengthened by extending them backwards over the bulb.

In this paper we have omitted all the evolutionary intermediates in both the formicine and dolichoderine lineages. Actually, we are quite fortunate in having most of these intermediates preserved in ants still living today. In Fig. 9 a dendrogram is shown, illustrating the principal steps in the evolution of the ant proventriculus. Note, for instance, how the development of sepals is clearly illustrated in the series *Notoncus*, *Cladomyrma*, *Camponotus*. Note also the evolution of the broadly reflexed cupola of *Iridomyrmex* from a small cap-like cupola as that of *Tapinoma*.

There remains to be considered one main type of proventriculus, found in some myrmecines, and in at least some dorylines, characterized by extreme degeneration.

THE REDUCED FORMICID PROVENTRICULUS: *ECITON*

In this proventriculus (Fig. 8), there remains no trace of the typical hymenopterous bulb as seen in *Myrmecia*. The cuticle at the level of what used to be the bulb ("bl.") is randomly and irregularly folded. Only the stomodæal valve is retained in unaltered form. This proventriculus is, in fact, nothing but a stomodæal valve, preceded by a posterior constriction of the crop.

It is clear here that we are dealing with a proventriculus that has departed radically from its usual fluid-pumping action. It may well be that this type of proventriculus has become modified to yield to the passage of solid matter. This possibility deserves further attention, especially since the dorylines and the myrmecines (some, but not all of which have similarly degenerate proventriculi) are known for their unusual feeding habits.

From the structure of this type of proventriculus it is clear that it cannot function as a passive dam. Damming, if at all occurring for long periods of time, must be dependent upon muscular contraction.

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